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XVIII. *Electro-Physiological Researches.*—Eleventh Series. *On the Secondary Electromotor Power of Nerves, and its Application to the Explanation of certain Electro-Physiological Phenomena.* By Signor CARLO MATTEUCCI. *Communicated by* General SABINE, *Treas. and V.P.R.S.*

Received June 2,—Read June 20, 1861.

THE object of this memoir is to describe experiments which prove that whenever a nerve is traversed by an electric current, it acquires in all its points a secondary electromotor power, and consequently becomes capable of producing in a conducting homogeneous circuit, whose extremities touch any two points whatever of that nerve, an electric current in a contrary direction to that of the current which we shall call the exciting current.

This property of nerves, which, as we shall see, is independent of their vital faculties, is nevertheless connected with their structure, and ceases when the integrity of that structure is impaired. All porous bodies, whether organic or inorganic, when saturated with a conducting liquid, are capable of acquiring a secondary electromotor power, so as to become a sort of secondary pile of RITTER; but I do not enter into an examination of these phenomena, which have been studied in their generality by other physicists, my principal aim being to determine exactly the conditions of the secondary electromotor power of nerves, in order to make a due application of these conditions to the explanation of the electro-physiological phenomena which are awakened at the opening of the voltaic circuit.

I shall begin by giving such a minute description of the experimental arrangements which I have followed as may enable others to repeat my experiments with ease, and furnish, as I believe, an unfailing method for conducting electro-physiological researches in general.

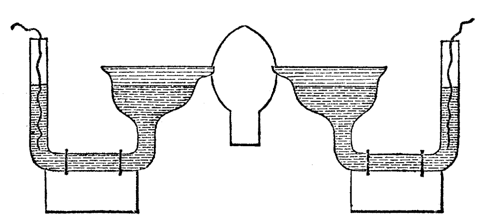
There is but one special instrument required in these researches, namely, a very delicate galvanometer, of from 24,000 to 30,000 coils of fine wire.

Many years ago I introduced in electro-physiological experiments the use of amalgamated zinc plates as extremities of the galvanometer, which may be employed much more easily and surely than the plates of distilled zinc proposed by JULES REGNAULT. I used also two small glasses, inside of which were fixed two thick strips composed of a great many layers of unsized paper or of flannel, forming a sort of cushion bent horizontally over the rim of each glass, like the cushions employed by DU BOIS REYMOND: these glasses were filled with a saturated solution of sulphate of zinc, into which were plunged the plates of amalgamated zinc. Before beginning the experiment, the two glasses were brought near to each other, so that the cushions were put in contact. If the slightest

sign of current was indicated by the galvanometer, the plates of zinc were amalgamated afresh, the cushions were carefully washed by agitating the glasses in a solution of sulphate of zinc, and the solution in the glasses was renewed. These preliminary arrangements having been made, the piece of muscle or nerve, the electromotor power of which was to be examined, was laid on a flat handle-shaped piece of gutta percha, and brought into contact with the two extremities of the cushions. After a certain number of experiments, between each of which it is necessary to ascertain that no current is developed when the cushions are put in immediate contact, it frequently happened that a certain alteration began to manifest itself; so that before the experiment could be continued, the zinc plates had to be amalgamated afresh, the cushions washed, and the solution in the glasses renewed as above described.

I have latterly succeeded in introducing some useful modifications in this method of experimenting, by means of which much trouble is saved, and the experiments are so simplified as to be executed rapidly, and at the same time with exactness.

Instead of two glasses, I now employ two tubes bent in the form of a U, one branch or arm of which is much larger than the other, and terminates like a funnel furnished with a broad flattened beak. These tubes are nearly filled with an amalgam of zinc, so dense as to be almost solid. A copper wire united to the galvanometer is inserted into the smaller branch of each tube and immersed in the amalgam. The large wide-mouthed branches of the tubes are filled up to the brim with the usual saturated neutral solution of zinc, so that the liquid extends in a very thin stratum over their flattened beaks. It is easy to lay on these beaks a single stratum of unsized paper, which becomes instantly soaked, and can be renewed without the least difficulty. Thanks to this improvement in the way of operating, I have been able to carry on a series of experiments for months together without any sign of the currents which used so frequently to be produced between the liquids in the glasses; there is no longer any need of amalgamating afresh the zinc plates, and when the solution in the tube requires renewal the operation is quickly performed.

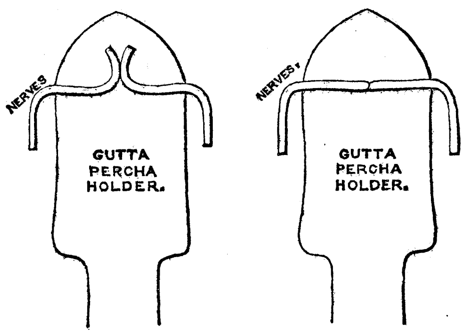


I shall describe, finally, an important part of the method pursued in these researches for comparing the electromotor power of different animal parts. This method (already well known, and which I have always followed in my electro-physiological researches*) is independent of the resistance of the elements themselves, and of the influence of time on animal structures; it consists in opposing two electromotor elements, and in observing the direction and intensity of the differential currents thus obtained. The two elements are laid on the gutta-percha holder, so as to place the two poles of the same name in contact. If, for instance, a comparison is to be made between the electromotor power of two pieces of frogs' thighs, a double pile is formed by bringing into contact the two transverse sections and closing the circuit, or *vice versâ* by touching the corresponding

* Philosophical Transactions, 1845.

extremities of the external surface of the two muscles with the extremities of the galvanometer. Thus it is found that the electromotor power of eight or ten elements or pieces of nerve of the same length is equal to that of a piece of muscle of the same length taken from the same animal.

I shall now describe the principal experiment made with the view of proving the development of secondary polarities in a nerve. Before commencing the experiment, I ascertained that no sign of current was obtained by touching any two points of a nervous filament, equidistant from its extremities, with the extremities of the galvanometer. I also ascertained that two sciatic nerves of a fowl or a rabbit, joined together either by bringing into contact the two distal extremities or the two proximal extremities, gave no sign whatever of current if these two nerves had not previously been subjected to the passage of electricity, and if the experiment had been properly prepared. By due preparation of the experiment, I mean it to be understood that the contact between the two pieces of nerve ought to be either between the two surfaces or the two transverse sections of these nerves, and never between the surface of the one and the transverse section of the other. In order to ensure this result, the two pieces of nerve should be laid on the gutta-percha holder, so as to establish the contact either of their surfaces or of their transverse sections on the middle of the holder, while the two opposite extremities of the nerves hang down over the two opposite sides of the holder.

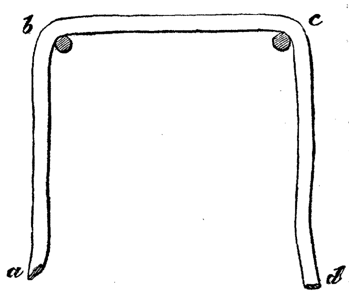


The leading experiment is performed either by laying a nervous cord upon two platinum wires, or by placing this cord upon two cushions of flannel or paper soaked with spring water, communicating with the poles of a pile. The experiment may also be made by preparing a fowl and a frog so as to leave their limbs united to the two sciatic nerves, and these nerves to a portion of the spine. An electric current from a pile of eight or ten elements is then sent through the nerves for a longer or shorter time. After the nerves have been thus traversed by the current, they are laid on the gutta-percha holder and put into communication with the galvanometer. The needle deviates, and indicates that the nerve is traversed, in the portion which was placed between the two electrodes, by a current the direction of which is opposite to that of the pile, and which lasts a certain time.

Signs of secondary current are also obtained by touching with the extremites of the galvanometer those portions of the nerve which have not been traversed by the current, that is, between the points touched by the electrodes and the points of the nerve which hang outside of the circuit. It is important to observe that the direction of the currents thus obtained is the same as that of the pile-current between the electrodes. I have constantly remarked that the current thus obtained between the points in proximity to the negative electrode and the external portion of the nerve on that side, is much

stronger than the current obtained between the points touched by the positive electrode and the external portion of the nerve towards this electrode.

In order to render this result more evident, I give the numbers obtained in several experiments in which the nerve had been subjected to the passage of the current, being laid upon two cushions. For the sake of brevity, let *a*, *b*, *c*, *d* be the nervous cord laid on the electrodes of a pile, these electrodes being indicated by *b* and *c*. After the passage of the current, I touch the extremities of the galvanometer with the points *b c*, or *b a*, or *c d* of the nerve. In all these cases the secondary current *b c*, obtained between the points *b* and *c*, has a contrary direction to that of the pile, and is invariably the strongest. The currents *a b* and *c d*, which are obtained in the portions of the nerve not traversed by the current, have the same direction as the pile-current; *b a* (that is, the current obtained between the points touched by the negative electrode and the free extremity of the nerve) is always greater than the current *c d* between the positive electrode and the other extremity of the nerve. The following are the numbers obtained:—



Sciatic nerve of a frog traversed during 60″ by a current of eight small elements (zinc, carbon, and salt water):—

Current *b c*	45°
a b	10
c d	4

Sciatic nerve of a sheep with a pile of eight elements during 60″:—

Current *b c*	72°
a b	37
c d	4

Sciatic nerve of a rabbit with a pile of eight elements for 60″:—

Current *b c*	70° to 80°
a b	35
c d	10

I give also the numbers obtained in experiments in which, instead of cushions as extremities of the galvanometer, I employed two platinum wires carefully depolarized between each experiment.

Sciatic nerve of a fowl with a pile of eight elements for 2 minutes:—

Current *b c*	25°
a b	16
c d	6

Sciatic nerve of a sheep in the same conditions as the preceding experiment:—

Current *b c*	90°
a b	38
c d	21

I shall not, as already said, enter here into particular considerations as to the production of secondary polarity in certain bodies more or less analogous to nerves, and which physically may be regarded as a solid porous mass the cavities of which are full of a conducting liquid. The general conditions required for the development of the secondary electromotor power of nerves leave no doubt as to the interpretation of this phenomenon: in the points of a nerve touched by the electrodes of a pile, the products of electrolysation are accumulated, and from thence spread through the tissue more or less, according to differences of its structure and chemical composition. The direction of the secondary current in a nerve is the same as that which is obtained after having sent a current through a strip of paper or flannel steeped in a weak saline solution, or, still more simply, by wetting two points of this strip, namely that which corresponds to the negative pole with an acid, the other, corresponding to the positive pole, with an alkaline solution, and then closing the circuit by touching with the extremities of the galvanometer either two intermediate points, or two points outside of those traversed by the current.

The object of this memoir is, I repeat, the study of secondary electromotor power in nerves, with a view to its application to electro-physiology. The principal experiment succeeds perfectly on the entire nerve of a living animal. It is easy to lay bare on a rabbit or fowl a long piece of the sciatic nerve, and to subject this nerve to the passage of a current; when the points of the nerve which have been traversed by the current are put in contact with the cushions of the galvanometer, currents owing to secondary polarities are immediately obtained.

By employing the differential method already described, I have also been enabled to prove that the secondary electromotor power of nerves is independent of their state of vitality. Thus I have compared two sciatic nerves of fowls, the one taken the instant the animal is killed, the other four days after death. These nerves, after being cut exactly of the same length, were placed one after another in the same conditions, and traversed by the same current for an equal time, after which they were laid on the gutta-percha holder and in opposition: no sign of differential currents was obtained.

I take the sciatic nerve of a sheep, measuring 210 millims., and lay its extremities on the electrodes of the pile. It is easy to imagine, without the aid of a figure, how a commutator may be employed in this experiment in order to close the circuit upon the nerve, either with the pile or with the galvanometer, by a rapid movement of the instrument. With the aid of this commutator, in a very small fraction of a second I have sent a current of from eight to ten of GROVE's elements through this long nerve, and this has sufficed to develope the secondary electromotor power in all points of the nerve. I have frequently repeated this experiment, touching successively different points of a long nerve with the extremities of the galvanometer kept at an equal distance. I obtained a secondary current in all these points, but as to intensity the results were not constant.

As far back as the time of my first experiments, I had observed that the secondary current obtained between two given points of the nerve differed according to whether

the experiment was made before or after having touched the nerve in other points; consequently in all my subsequent experiments I have never employed any other method than the differential method which I have already described.

I prepare on a fowl two sciatic nerves, and lay them side by side on the two cushions of glasses filled with spring water, in which I plunge the electrodes of a pile of ten small elements (zinc, charcoal, and salt water). The current divides itself equally between the two nerves. I leave the circuit closed for a time, varying from five to twenty minutes. I then lay the two nerves in opposition on the gutta-percha holder, and bring them into communication with the galvanometer. No trace of differential current is to be detected, while each of these nerves gives a secondary current of from 40° to 50°.

I shall now describe briefly the results obtained by studying the influence exercised by various physical and chemical conditions, to which the nerve was subject, on its electromotor power.

I prepare in the usual way two sciatic nerves of a fowl. I put one of these nerves into a glass tube, which is left for fifteen minutes in a refrigerating mixture; at the end of this time the nerve thus cooled is exposed to the air until it acquires the same temperature as the other nerve. Both nerves are then disposed so as to be traversed by the same current, after which they are reunited in opposition and tested at the galvanometer. I find that the secondary electromotor power of the nerve which had been cooled had suffered great diminution.

I take two similar sciatic nerves, and immerse one of them in water at $+50°$ or 60° C., leaving the other nerve intact. I send a current, as in the former experiment, through both nerves, and find the secondary electromotor power strongest in the nerve which was not heated.

I prepare on another fowl two other sciatic nerves; I crush or compress one, and leave the other intact. After these two nerves have been simultaneously subjected to the passage of the current, the secondary electromotor power is greatly weakened in the nerve which has been crushed.

Portions of sciatic nerve which have been held for a few minutes in an alkaline solution containing $\frac{1}{2000}$ weight of potassa, lose completely their secondary electromotor power. Immersion of the nerve in alcohol produces the same result. If the nerve is kept for a very long time in distilled water, the secondary electromotor power is weakened. It is remarkable that the time which may elapse after the passage of the electric current in the nerve and the washing of the nerve in water, exercises no influence on the secondary electromotor power of the nerve. If two sciatic nerves are exposed to the same current, but successively, no difference is found between them even when there has been an interval of from fifteen to twenty minutes between the electrolysation of the two nerves. After having subjected two similar nerves to the passage of the current, if one of them is afterwards held for a few seconds in distilled water, its secondary electromotor power is unaltered.

A nerve subjected to the passage of the current, first in one direction and then in

the contrary direction, for an equal time, acquires in the second case a weaker secondary electromotor power than it would have acquired had it been taken in its natural condition.

The duration of the passage of the current increases, within certain limits, the secondary electromotor power of a nerve. I have proved the influence of the intensity of the current, by putting successively in the circuit a single nerve, and then two nerves joined together, so that the intensity of the current was always half for each of the latter. This experiment was made with two, six, and twelve elements of GROVE. After each experiment, I sought the differential current by confronting the nerve traversed by the whole with that traversed by the half current. The differential currents were 3°, 28°, and 38°.

I have also proved that neither the size nor the number of the nerves united by superposition exercised any influence on the secondary electromotor power. After having subjected four similar nerves to the same current, I made a differential pile, setting three of these nerves superposed in opposition to one; and no differential current was produced. I have sent the same current through the nerve of a frog, that of a lamb, and of a fowl. These nerves were of the same length; and in order to avoid the desiccation of the nerve of the frog especially, they were placed under a moistened glass bell. After they had been electrolysed, I opposed successively the nerve of the frog to that of the fowl, the nerve of the fowl to that of the lamb, and so on: I found no differential current. Yet each of these nerves, taken separately, gave a current of from 40° to 50°, due to secondary polarity.

I would again recall attention to the result obtained in studying the influence of the length of nerves. In whatever way the experiments were made, whatever might be the nerves employed, a strong differential current was constantly found in the direction of the longest piece of nerve. We shall afterwards see how this result is modified, according to whether the two species of nerve of unequal lengths to be compared have been taken near the positive or near the negative electrode; these differences do not, however, alter the general result already referred to. The experiment consists in sending the current through a long nerve, like the sciatic nerve of a lamb. This nerve is electrolysed and divided into four equal parts, three of which are left disposed as they were during the passage of the current, and the remaining one is opposed to these three. This experiment was performed by alternating the position of the pieces; a differential current of from 30° to 40° was constantly obtained, owing to the longest piece. The same effect is obtained from nerves of frogs and fowls, whether the operation of cutting the nerve has been made after being electrolysed or before. This result cannot be understood unless we admit that the secondary electromotor power, which originally is greatest in contact with the electrodes, extends successively to all the parts of a nerve traversed by the current.

I come now to the fact which I consider as most important in the application of secondary electromotor power to the explanation of certain electro-physiological phenomena. This fact is resumed in the following proposition:—

The secondary electromotor power of a nerve is not equal in all points of the nerve,

being much stronger in the portion of the nerve near the positive electrode, than in the portion near the negative electrode: this difference is greater in a nerve traversed by the current in the direction contrary to that of its ramification, than in a nerve traversed by the current in the direction of its ramification.

I have verified this proposition by experiments on sciatic nerves of fowls, frogs, and rabbits. I begin by laying two sciatic nerves of equal length on the cushions of two glasses filled with spring water. These nerves are disposed in the same way as to their ramification, that is, the voltaic current in both nerves must be either direct or inverse. After the passage of the current, the two nerves, each of which has been traversed by one half of the current, are opposed to each other in the usual way on the gutta-percha holder. I never found any indication of differential current, although each of these nerves, taken separately, gave a very strong secondary current, having the same direction whatever might be the position of the two points of the nerve touched by the extremities of the galvanometer.

In order to show the difference of secondary electomotor power taken at points of the nerve nearest to the two poles, I cut an electrolysed nerve into two equal parts, and oppose these parts to each other; a differential current of 25 to 30 and more degrees is constantly obtained from the portion of nerve nearest to the positive pole. This experiment was made on a long sciatic nerve of a lamb. After having electrolysed this nerve, I cut it into a certain number of equal parts, which I opposed to each other, and I found constantly a differential current of 25° to 30° and more from the portion of nerve near the positive electrode.

The experiment was again made on a long sciatic nerve of a lamb. This nerve, after having been electrolysed, was cut into a certain number of equal parts, which were then set in opposition two by two and tested with the galvanometer. The differential current obtained for each couple was always determined by the portion of nerve near the positive electrode; and this intensity increased with the distance which separated the two pieces of nerve considered in relation to their natural position.

The influence exercised by the direction of the current which developes secondary electromotor power in a nerve, relatively to its ramification, may be demonstrated by repeating the experiment, already so often described, upon two sciatic nerves taken from a fowl or other animal, with this difference, that the two nerves (laid side by side) must be disposed so that the current may traverse one nerve in the direction of its ramification, and the other nerve in the opposite direction. As the current is divided in half, if these nerves, after having been electrolysed and then set in opposition, present a differential current, this current must be attributed to a difference of effect corresponding to the direction of the current through the nerves relatively to their ramification. This result is obtained either by opposing the two entire nerves, or, still better, by dividing one of these nerves into two equal parts and opposing these halves.

In a great number of similar experiments performed on nerves of different animals, I have constantly found a differential current, by which it is proved that a nerve traversed

by the current in a direction contrary to that of its ramification (*inversely*, as it is called in electro-physiology) had acquired a stronger electromotor power than that acquired by a nerve traversed in the direction of its ramification. Naturally, owing to a difference in the length, and consequently in the resistance of the nerve, this differential current must be stronger when the experiment is made on the two halves of a nerve than on two entire nerves. The same result may be obtained with different arrangements of the experiment. One of these arrangements consists in taking rapidly from a fowl the two nerves of the thigh, and in disposing these nerves one after another as they were in the living animal, so that the current traverses the one in the same direction as the ramification, and the other in the opposite direction. After being traversed by the current, the nerves are put in opposition: a differential current is determined by the nerve which, for the sake of brevity, we shall call *inverse*.

Here, once for all, I observe that in making these comparative experiments it is necessary to have a galvanometer and a rheostat in the circuit, in order to obtain constantly the same pile-current.

Another analogous way of performing this experiment is to employ a prepared animal such as is used in the electro-physiological experiment which demonstrates the influence exercised by the direction of a continuous current on the irritability of a nerve. As is well known, this preparation consists of the two limbs of an animal united by the two nerves of the thighs connected with a portion of the spine. The extremities of the limbs are immersed in water contained in two glasses, together with the electrodes of the pile; and thus the current goes from one limb to the other, traversing the two nerves, inversely in the nerve next the positive electrode, and directly in the other nerve, next the negative electrode. This experiment may be made on living animals, that is, with the entire trunk, and on animals such as frogs, fowls, and rabbits recently killed, by prolonging the passage of the current from a few seconds to twenty or thirty minutes, according to its intensity. Both the nerves acquire a strong secondary polarity; but the *inverse* nerve acquires a stronger secondary electromotor power than the *direct*, and in both nerves the secondary electromotor power is greater in the portion near the positive electrode than in that which is near the negative electrode.

The object of these researches was not, as we have said, to study the production of secondary electromotor power in nerves rather than in other porous and humid bodies of various structure and chemical composition. Under this point of view it is evident that the phenomenon is complex and its analysation difficult. In the present state of science, therefore, we are unable to account for the differences presented by a nerve in its different points, according to their proximity to one pole or the other, and according to the direction in which the nerve is traversed by the current. It is possible that similar differences will present themselves in other bodies which are not organized, or taken from living animals. It is sufficient for my present object to have proved that the secondary electromotor power of a nerve requires for its development the integrity of structure of the nerve itself, but not the excitability of the living animal, and to have determined

rigorously those differences of this power which have led me to ground the explanation of the electro-physiological phenomena which take place on the opening of the circuit on a fundamental physical fact.

The arrangement which I have for a long time adopted in the study of these phenomena is well known, and has been described in several works on physics and physiology.

This arrangement consists of a frog prepared after the usual manner of GALVANI, and then cut in half at the symphysis of the pelvis. If a continuous current is passed from one limb to another for fifteen, twenty, or thirty seconds, according to the force of the current, it is known that the opening of the circuit is accompanied by violent contractions of the limb traversed by the inverse current. These contractions depend, as I showed many years ago*, on a particular state of the nerve; and in fact the contractions are obtained and continue when the circuit is interrupted by cutting the nerve near the spine, but they are no longer produced if the nerve is cut near its insertion in the muscles of the leg.

My object in this memoir has been to prove that the particular state of the nerve above described consists of secondary electromotor power, that is, in a well-known physical phenomenon.

I complete this demonstration by a very simple experiment. After having passed a current through two lumbar nerves of a fowl in the way already described, I lay the nerve of a galvanoscopic frog on different points of these nerves, precisely at the instant in which I open the circuit: I employ several galvanoscopic frogs in order to test with their nerves different points of the nerves of the fowl, and I also vary the direction of the nerves of the galvanoscopic frogs upon the nerves of the fowl. The instant that I open the circuit, the galvanoscopic frogs contract; these contractions are also produced on touching the nerves of the fowl with the galvanoscopic frogs some instants after the opening of the circuit. Thus the secondary current, the existence of which is demonstrated by the galvanometer, and which is *direct* for the nerve that has been traversed by the *inverse* current, is also demonstrated by the contractions of the galvanoscopic frog: this direction of the secondary current explains, according to the known laws of electro-physiology, the effects produced by it on the opening of the circuit.

The differences of electromotor power found in various points of the electrolysed nerve, the prevalence of this power in the portions of the nerve near the positive electrode, very probably also the different degree of this secondary electromotor power in the various *strata* which compose the interior and the envelope of the nerve, explain sufficiently the secondary current which takes place in the nerve at the opening of the circuit, and which is *direct* and most intense in the nerve which has already been traversed by the inverse current in proximity to the positive electrode.

In conclusion, in order to explain the physiological effects which accompany the opening of a circuit, we must henceforth recur to the secondary electromotor power which is developed in nerves, and to the laws of this phenomenon.

* Electro-Physiological Researches, Fifth Series, Part II.—Phil. Trans. for 1847, pp. 235, 236.